

Fisheries-induced evolution of body size and other life history traits: the impact of gear selectivity

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Abstract

Commercial fishing utilizes a variety of gears, all of which are selective with respect to at least some phenotypic characteristics of individuals such as body size or girth. Empirical evidence is mounting that such fishing induces rapid evolutionary changes, with consequences for the size structure and dynamics of the exploited stocks. Here we present the results of life-history models designed to study fisheries-induced evolutionary changes in body size at maturation, growth, and reproduction in a stock fished by different gear types. We examine evolutionary endpoints of, and selection pressures on, three corresponding life-history traits. We show that fishing usually selects for earlier maturation at smaller size, higher reproductive investment, and faster growth. This is especially true for trawl-like gears, which are primarily size-selective and remove large fish. On the other hand, gears that only remove fish within a certain size slot, such as gillnets, can lead to evolutionary bistability and evolution of delayed maturation. Moreover, gears that are also directly selective on behavioral traits influencing growth, such as baited lines, can lead to slower growth. Our results also highlight how the evolutionary effects of fishing are sensitive to changes in mesh size and fishing mortality, commonly regulated in fisheries management.

Keywords: life histories, maturation, reproductive investment, growth rate, trawls, gillnets, baited lines

Introduction

Empirical evidence is mounting that fisheries induces rapid evolutionary changes, with consequences for the structure and dynamics of the exploited stocks (Jørgensen et al. 2007). Fishing always selects on some phenotypic characteristics and traits of individuals, either directly or indirectly. Many gears used in commercial fisheries, among them trawls, gillnets and traps, select directly on body size or girth because they use mesh sizes and escapement devices that retain only a certain range of body sizes or girths (Heino & Godø 2002). Other fishing gears that are based on attraction to bait, such as baited lines or traps, might attract mostly faster-growing fish that need to forage more actively, and therefore directly select on individual growth rates (Miller 1957, Favro et al. 1979, Heino & Godø 2002). Direct selectivity on some individual traits might indirectly affect other traits. For example, it has been hypothesized that selective removal of large fish might favor slow-growing phenotypes since slower-growing individuals would enter the fishery later (Miller 1957, Favro et al. 1979).

A broad range of theoretical models of varying complexity have been trying to elucidate the most likely evolutionary consequences of fishing: Which traits are most likely to be affected? Which of them are liable to the fastest and/or largest changes? As part of this ongoing research, we show here that different types of gears used in commercial fishing can lead to disparate evolutionary responses, which depend on the fishing intensity and selectivity of the gear.

Models

Ecological and evolutionary setting before the start of the fishery

Here we use a relatively simple life history model to study fisheries-induced evolutionary changes in body size at maturation, growth, and reproduction. We compare the results for a fish stock which lives in a seasonal environment and reproduces once a year. In the results shown below, only the recruitment is density dependent, following a Beverton-Holt relationship, while growth and fecundity of individual fish are density independent. Under such conditions, evolutionarily stable life histories can be found by maximizing the expected lifetime reproductive output, R_0 , without accounting for density dependent feedback (Mylius and Diekmann 1995). The model assumes a monomorphic population and examines evolutionary endpoints of, and selection pressures on, several corresponding life-history traits.

We use an extension of the model of individual growth proposed by Lester et al. (2004), in which the individual growth, measured in body length, is linear in juveniles and follows a von Bertalanffy growth curve after maturation, and the gonadosomatic index (GSI, defined as the ratio of gonad weight to somatic weight) is independent of size in the adults. Moreover, we assume that the growth increments are limited by a certain maximum physiologically feasible annual growth increment (see below), and that the maturation process can be described by a size-dependent but age-independent probabilistic maturation reaction norm (PMRN, Heino et al. 2002). This type of PMRN is characterized by a reaction norm midpoint, which represents an individual body size at which the probability of maturation equals 50%, and reaction norm width, which characterizes the range of sizes across which the individuals can mature.

Individual fish in our model face two fundamental trade-offs, between growth and survival in juvenile and adult fish, and between somatic growth and reproduction in adult fish. That is, faster growth is traded off against increased growth-related mortality, for example due to increased time spent foraging and thereby increased exposure to predators, and higher size-specific fecundity is traded off against slower growth after maturation.

The fish are characterized by three life history traits that can evolve: PMRN midpoint, GSI, and the growth effort. We express growth in relative terms: the effort represents the fraction of the maximum physiologically feasible growth that is actually used for somatic growth in juveniles and split between somatic growth and reproduction in the adults. Growth effort equal to 0 means that the individuals do not grow, but they also do not suffer from growth-related mortality. Growth effort equal to 1 characterizes individuals that reach the physiological limit; we assume that this limit (set to 50 cm in the example below) leads to 100% growth-related mortality.

Evolutionarily stable life history in the absence of harvesting is largely determined by the strength of natural mortality (Roff 1983, Taborsky et al. 2003, Lester et al. 2004). In the example below we assume size-dependent natural mortality that yields an optimal life history with PMRN midpoint at 155 cm, GSI of 0.264, and growth effort of 0.434 (i.e., the annual size increments of juvenile fish are ca. 22 cm and the PMRN midpoint corresponds to maturation at the age of ~7.1 years).

Characteristics of the fishing gears

We harvest this fish stock with three different gears: ‘trawls’, ‘gillnets’, and ‘baited lines’. In all cases, harvesting occurs once a year with a fixed effort. We assume that the trawls and gillnets are only size-selective, while the baited lines combine a trawl-like size selectivity with direct selectivity on the growth rate. The rationale behind this assumption is that smaller fish can be more difficult to hook or that they might not be attracted by the bait.

The trawls are characterized by a sigmoidal selection curve with threshold size (H_T), selectivity slope (σ_T , set to 10 cm in all simulations), and maximum annual harvesting probability (h_{\max}), such that the harvesting probability for fish of length L equals

$$h_T(L) = h_{\max} / (1 + e^{(H_T - L)/\sigma_T}).$$

The gillnets are characterized by a selection curve that has the shape of a normal distribution with the mean or target size (H_G), variance (σ_G^2 , set to 1,000 cm² in all simulations), and maximum annual harvesting probability (h_{\max}). The harvesting probability for fish of length L equals

$$h_G(L) = 2h_{\max} / (1 + e^{(L - H_T)^2/\sigma_G^2}).$$

The baited lines combine the sigmoidal size-selectivity (with the threshold set at $H_T=150$ cm and slope $\sigma_T=10$ cm) with an increasing selectivity with respect to growth effort:

$$h_B(g, L) = \min[1, C_{\max} g^x / (1 + e^{(H_T - L)/\sigma_T})],$$

where the exponent (x) scales the selectivity of the gear with respect to growth ($x=1$ means that the probability of being caught increases linearly with growth effort in fish of the same size, while a very high exponent means that in practice, only individuals with very high growth effort can be caught) and C_{\max} scales the maximum harvesting probability.

We vary two characteristics of each gear in the simulations: the threshold size H_T and maximum annual harvesting probability h_{\max} for trawls, the target size H_G and maximum annual harvesting probability h_{\max} for gillnets, and the scaling of the growth selectivity x and harvesting probability C_{\max} for baited lines. The results are thus not directly comparable with respect to total fishing pressure (e.g., in terms of annual harvest or escapement) among and within gears.

We use two measures of evolutionary change in the model: normalized selection gradient and evolutionary endpoints. We express the selection gradient for each trait as the slope of the fitness function for each trait (in our case, we equate fitness to the expected lifetime reproductive output R_0) and normalize it by multiplying the slope by the (mean) trait value. This normalized selection gradient is therefore a dimensionless number that, for each trait, expresses the relative propensity to change under a given exploitation pattern.

We then identify all possible evolutionary endpoints that can arise under a given fishing regime by finding all evolutionarily stable life history strategies; in our model with density-independent growth, these strategies correspond to local fitness maxima.

Results

We show that initially, fishing usually selects for earlier maturation at smaller size and higher reproductive investment. Growth rate might initially increase, as in trawls, or decrease, as in some results for the baited lines (Fig. 1). Overall, the magnitude of the normalized selection gradient is largest for the PMRN midpoint and lowest for GSI, suggesting that the initial evolutionary response to fisheries-induced selection is most likely fastest (in relative terms) in size at maturation and slowest in reproductive investment when we compare the three traits under selection.

Often, the evolutionary endpoints cannot be inferred from the initial response. First, there is no one-to-one correspondence between the normalized selection gradient and the difference between the initial and final trait value when comparing the effects of different harvesting scenarios for each trait (see, e.g., the selection gradient and endpoints for GSI in a trawl fishery in Figs. 1 and 2). Even more surprisingly, selection gradient and evolutionary endpoints might differ qualitatively. In trawls and gillnets, growth effort might increase or decrease initially but the evolutionary endpoints are always characterized by an increased growth effort. The same holds for gillnets and GSI. On the other hand, the selection gradient of growth effort is always negative for baited lines, but growth effort might eventually decrease or increase (Figs. 1 and 2). These two types of mismatch stem from the fact that multiple traits are evolving simultaneously, and the path from the initial trait combination to the evolutionary endpoint might not be a straight line but can often represent a convoluted trajectory in the high-dimensional trait space.

The most complicated results in terms of evolutionary endpoints occur in gillnets. Since gillnets preferentially remove individuals within a certain size slot, they can favor evolution of two different life history strategies: early maturation well below the range of sizes targeted by the gillnet fishery, or late maturation well above the range. We therefore see discontinuous and bistable responses in the PMRN midpoint, GSI and growth effort to varying fishing pressure across a range of target sizes and harvesting probabilities. Gillnets are also the only gear in our example which can actually induce evolution towards later size at maturation and lower reproductive investment, although this outcome requires relatively low fishing mortality targeting immature fish (Fig. 2).

Concluding remarks

We show that the evolutionary effects of fishing will strongly depend on the selectivity of the fishing gear. Initial, short-term evolutionary responses (increasing or decreasing trait values and the relative rate of change) can be quantitatively and qualitatively different from long-term changes and evolutionary endpoints. This finding can have important repercussions for evolutionary enlightened management of exploited fish stocks (Jørgensen et al. 2007). Our results also highlight how the evolutionary effects of fishing are sensitive to changes in mesh size and fishing mortality, commonly regulated in fisheries management. Our comparison of different gears indicates that the least amount of evolutionary change occurs for harvesting with low overall intensity, e.g., when the fishery targets only very large fish. Thus, we reiterate the need for reduced fishing pressure in overexploited fish stocks (Pauly et al. 2002). Using individual-based, eco-genetic models (Dunlop et al. 2007), we will also analyze how different gears affect life history traits over decadal time scales, the latter being especially relevant for fisheries management.

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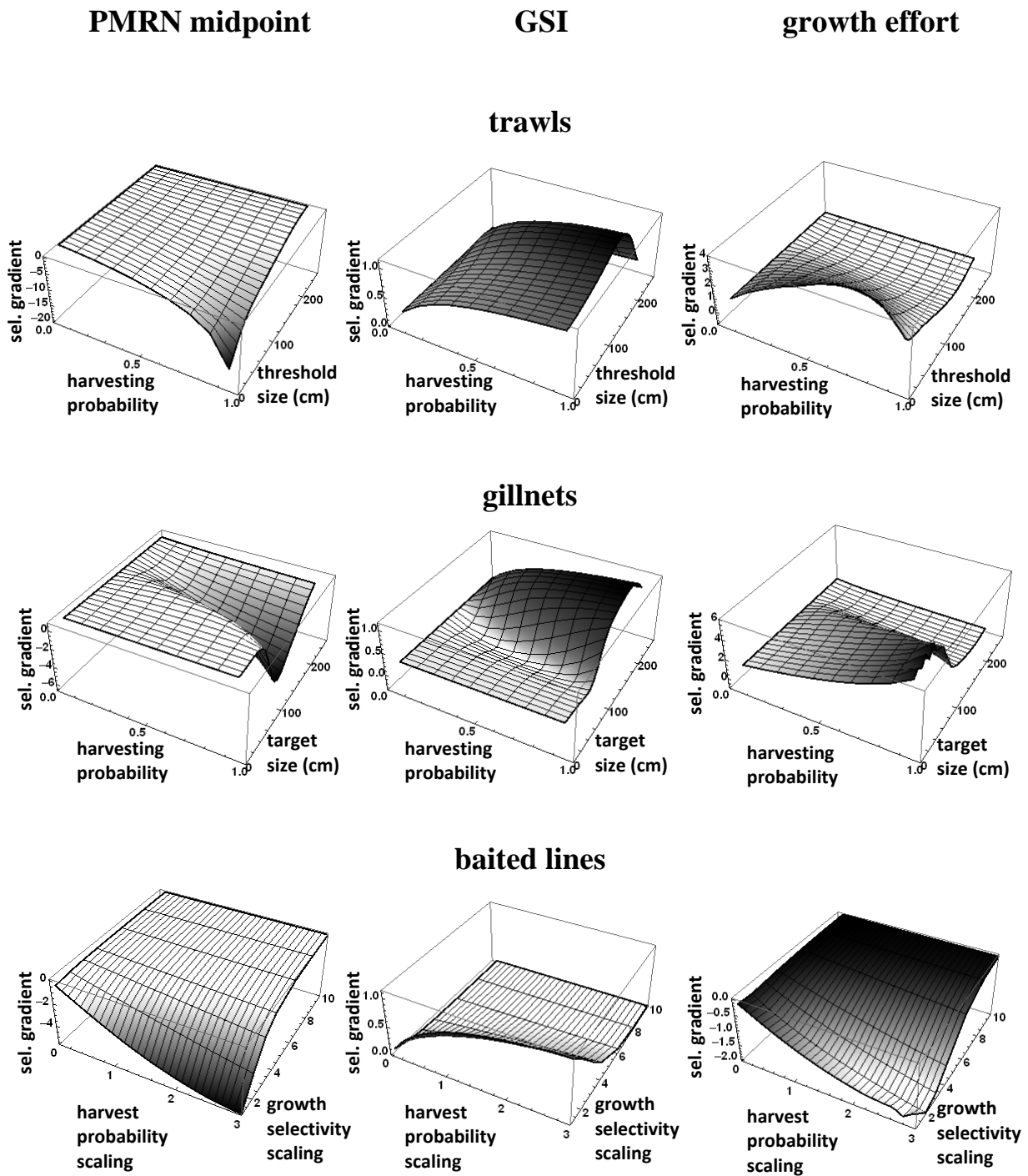


Figure 1: Normalized selection gradients for size at maturation (PMRN midpoint, left column), reproductive investment (GSI, middle column) and growth effort (right column) as a function of the harvesting intensity and gear selectivity. The selection gradients are evaluated for a life history that is evolutionarily stable in the absence of harvesting; see text for details. Upper row: trawls; middle row: gillnets; bottom row: baited lines. Results based on a life history optimization model when all density-dependence affects recruitment and individual growth is density-independent.

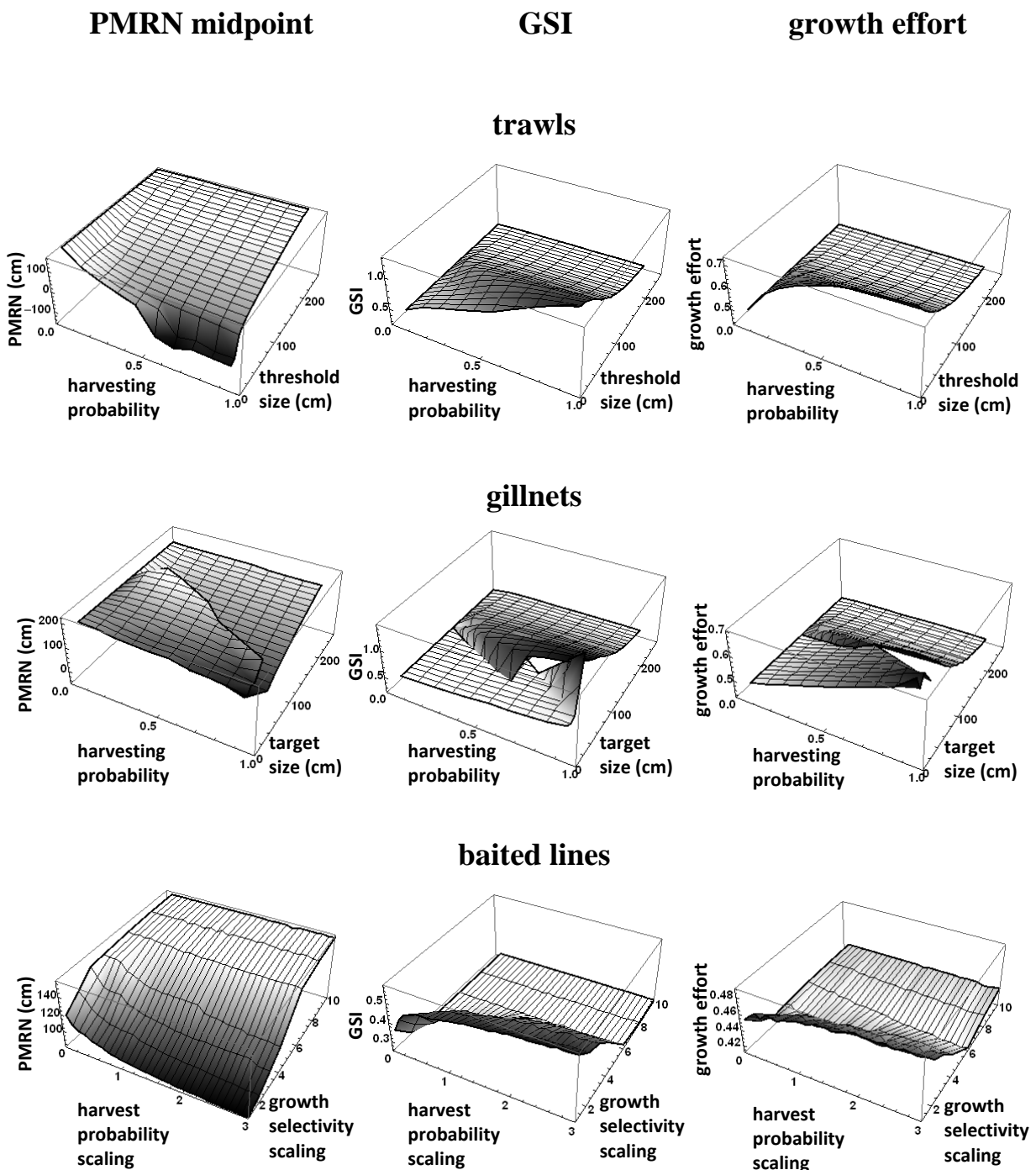


Figure 2: Evolutionary endpoints for size at maturation (PMRN midpoint, left column), reproductive investment (GSI, middle column) and growth effort (right column) as a function of the harvesting intensity and gear selectivity. Two different endpoints are possible for some combinations of maximum harvesting probability and target size of gillnets; see text for details. Upper row: trawls; middle row: gillnets; bottom row: baited lines. Results based on a life history optimization model when all density-dependence affects recruitment and individual growth is density-independent.